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Incremental Enamel Development in Modern Human Deciduous Anterior Teeth

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KEY WORDS age-at-death; cusp formation times; daily enamel secretion rates; developmental biology

ABSTRACT This study reconstructs incremental enamel development for a sample of modern human deciduous mandibular ($n = 42$) and maxillary ($n = 42$) anterior (incisors and canines) teeth. Results are compared between anterior teeth, and with previous research for deciduous molars (Mahoney: Am J Phys Anthropol 144 (2011) 204–214) to identify developmental differences along the tooth row. Two hypotheses are tested: Retzius line periodicity will remain constant in teeth from the same jaw and range from 6 to 12 days among individuals, as in human permanent teeth; daily enamel secretion rates (DSRs) will not vary between deciduous teeth, as in some human permanent tooth types. A further aim is to search for links between deciduous incremental enamel development and the previously reported eruption sequence. Retzius line periodicity in anterior teeth ranged between 5 and 6 days, but did not differ between an incisor and molar of one individual. Intradian line periodicity was 12 h. Mean cuspal DSRs varied slightly between equivalent regions along the tooth row. Mandibular incisors initiated enamel formation first, had the fastest mean DSRs, the greatest prenatal formation time, and based upon prior studies are the first deciduous tooth to erupt. Relatively rapid development in mandibular incisors in advance of early eruption may explain some of the variation in DSRs along the tooth row that cannot be explained by birth. Links between DSRs, enamel initiation times, and the deciduous eruption sequence are proposed. Anterior crown formation times presented here can contribute toward human infant age-at-death estimates. Regression equations for reconstructing formation time in worn incisors are given. Am J Phys Anthropol 147:637–651, 2012.

The timing [daily enamel secretion rates (DSRs), Retzius and intradian line periodicity, pre-, and postnatal cusp growth, and crown formation time (CFT)] of enamel development can be reconstructed from incremental growth markings that are retained in teeth after death (e.g., Boyde, 1964a,b; Dean, 1987a; Beynon et al., 1991a; Dean and Beynon, 1991; Dean et al., 1993). In comparative studies of primate permanent dentition some of these variables are regularly reconstructed to examine the mechanism that underlies the morphological development of tooth enamel (e.g., Dean et al., 1986; Macho et al., 1996; Schwartz et al., 2005; Mahoney et al., 2007; Smith et al., 2007a; Lacruz et al., 2008). Such studies provide key insights into the evolution of primate dentition and life history, as well as the biological rhythms that regulate hard tissue development (e.g., Bromage and Dean, 1985; Dean et al., 2001; Schwartz et al., 2002; Smith et al., 2007b; Bromage et al., 2009).

Others have reconstructed the timing of permanent incremental enamel development along the tooth row (e.g., Beynon et al., 1991b; Dirks, 1998; Reid et al., 1998a,b; Dirks and Bowman, 2007; Smith et al., 2007a) to reveal variation between primates (e.g., Dirks, 2003), which can contribute to an understanding about species differences in life history (e.g., Dirks and Bowman, 2007). Although some previous researchers have described human deciduous incremental enamel development along the tooth row (e.g., FitzGerald et al., 1999; Birch and Dean, 2009; FitzGerald and Hillson, 2009; Mahoney, 2011), the topic has generally received limited attention. Nevertheless, there are clear differences in the environment in which human deciduous and permanent teeth grow which could influence incremental enamel development. For example, unlike human permanent tooth enamel, all human deciduous enamel commences development in utero (e.g., Kraus and Jordan, 1965). Since deciduous incisor enamel develops in advance of molars, birth is recorded at different times in these different tooth types (e.g., Kraus and Jordan, 1965). Birth is an influence on DSRs in deciduous enamel, temporarily reducing postnatal rates (e.g., Macchiarelli et al., 2006; Birch and Dean, 2009; Mahoney, 2011). Thus, it would seem likely that DSRs from deciduous incisors might differ when compared with equivalent regions in deciduous molars. If so, then this would contrast with the situation reported for human permanent teeth where mean DSRs generally remain constant between some tooth types (Beynon et al., 1991b).

Another aspect of human deciduous incremental enamel development that has received limited attention in the literature is Retzius line periodicity. The periodic nature of enamel formation produces a long period incremental marking known as a Retzius line (see Background review below). The majority of previous studies on human permanent teeth have demonstrated that the number of days of enamel formation between adjacent

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Retzius lines (the periodicity) remains constant within a tooth (FitzGerald, 1998; Mahoney, 2008), does not vary between teeth from the same jaw (e.g., Dean and Beynon, 1991; FitzGerald, 1998; Reid et al., 1998a; also see Dean and Scandrett, 1995 for corresponding dentin lines), but ranges from 6 to 12 days between individuals (e.g., Fukuhara, 1959; Beynon and Reid, 1987; Beynon, 1992; Reid et al., 1998a; Reid and Dean, 2000; Schwartz et al., 2001; Reid and Ferrell, 2006; Mahoney, 2008). One would expect similar findings in human deciduous teeth, thought this is not clear from the very few studies that have reported such values. Mahoney (2011) reported one value of 9 days for one deciduous second molar. As part of their study, Huda and Bowman (1994, 1995) reported a range of values from 4 or 5 days (depending on the observer) to 8 days for one canine and two deciduous molars, but this included variation within a tooth. If the lowermost value and the variation within the deciduous teeth in that study are confirmed, this would differ compared with findings reported in the majority of prior studies on human permanent teeth. No study has compared Retzius line periodicity between human deciduous teeth from the same jaw.

The aim of this study is to reconstruct the timing of incremental enamel development in a sample of modern human deciduous maxillary and mandibular anterior teeth (di_1, di^1, di_2, di^2, dc_1, and dc^1). As this will be the first study to comprehensively examine these tooth types in this way, these rarely reported developmental variables (e.g., Retzius and intradian line periodicity, enamel initiation times, CFTs) can be reused for comparisons with deciduous teeth from fossil species, which are hardly ever undertaken (e.g., Beynon et al., 1998a). The anterior CFTs can also contribute toward age-at-death estimations for human infants. Following this, results for the anterior teeth will be compared with previous findings for deciduous molars (Mahoney, 2011) to reconstruct incremental enamel development along the tooth row. The comparative molar data will be supplemented with additional new data presented here for Retzius line periodicity in molar teeth from the same jaw. The hypotheses tested are, DSRs will not vary along the deciduous tooth row, as in some human permanent tooth types (e.g., Beynon et al., 1991b); Retzius line periodicity will remain constant in teeth from the same jaw and range from 6 to 12 days between individuals, as in human permanent teeth (e.g., Reid et al., 1998a; Mahoney, 2008).

A further aim is to search for links between enamel initiation times along the tooth row (as well as other aspects of incremental development), and the previously documented eruption sequence for human deciduous teeth. Beynon et al. (1991a) proposed that aspects of incremental development in permanent teeth from a juvenile gorilla reflected mean tooth emergence times. This idea is tested here on human deciduous teeth. Methodological suggestions for recording incremental markings in deciduous teeth will also be given, which can guide future sample selection.

BACKGROUND

Incremental enamel markings

Rhythmic variations in the matrix secreted by enamel forming cells (ameloblasts) produce several types of incremental markings: cross-striations; Retzius lines; intradian lines; accentuated markings. Cross-striations, or short period markings, are the result of a daily (24 h) variation in ameloblast activity in humans (Asper, 1916; Schour and Poncher, 1937; Boyde, 1979, 1989; Risnes, 1986; Antoine et al., 2009), macaques (Bromage, 1991; Smith, 2006), and other animals (Mimura, 1939).

Retzius lines (Retzius, 1837), or long period markings, represent the successive location of the forming enamel front (Dean, 1987b; Risnes, 1990). Retzius line periodicity in permanent teeth is positively correlated with body mass in several extant and fossil primate taxa, as well as a sample of Proboscidea (Smith, 2008; Bromage et al., 2009), though some recently extinct lemurs are an exception (Schwartz et al., 2002).

Intradian lines are subdaily incremental markings (Gustafson, 1959; Boyde, 1989). They have been identified in human permanent enamel (FitzGerald, 1996; Lacruz and Bromage, 2006, their Fig. 1), and have a 12-h periodicity (time elapsed between adjacent intradian lines) in macaque enamel (Shellis and Poole, 1977; Smith, 2004). Studies of dentin suggest that intradian line periodicity, like Retzius line periodicity, may not be constant between species. For example, a periodicity of 12 h has been reported for human dentin (Kawasaki et al., 1979), 8–12 h for rabbits (Rosenberg and Simmons, 1980), and 8 h for rats (Ohtsuka and Shinoda, 1995).

Accentuated markings, (also called accentuated Retzius lines or Wilson bands), can form in developing enamel in response to systemic and psychological stress (e.g., Boyde, 1989; Goodman and Rose, 1990; Schwartz et al., 2006). Birth is thought to produce an accentuated marking, which has been named the neonatal line (Rushton, 1933; Schour, 1936; Weber and Eisenmann, 1971; Sabel et al., 2008). This line, and subsequent accentuated markings (e.g., Beynon et al., 1991b), can be used with cross-striations and Retzius lines to calculate pre-, and postnatal enamel formation time, and also to determine the growth sequence between teeth (e.g., Beynon et al., 1991a; Macho et al., 1996; Reid, 1998a,b; Schwartz et al., 2005, 2007).

Previous studies of deciduous enamel development

Enamel secretion rates. Early studies reported differences in growth rates between the deciduous and permanent teeth of one individual (Schour and Poncher, 1937), and more rapid calcification in deciduous central incisors compared with lateral incisors and molars in a sample of fetal cadaver jaws (Kraus, 1959a). Further knowledge of the relationship between enamel secretion rates and the position of a tooth along the dental row has been gained from recent studies of incremental enamel development that calculated DSRs from cross-striations. Fitzgerald and Hillson (2009), like Kraus (1959a), identified differences in mean DSRs (rates pooled from different enamel regions within a tooth) calculated from mainly prenatal enamel in a sample of deciduous incisors compared with first molars.

Others have reported DSR variation within deciduous teeth. Birch and Dean (2009) found that mean DSRs in mandibular incisors (central and lateral combined) and canines differed depending upon the region of the tooth examined. Rates were lowest near the enamel–dentin junction (EDJ), fastest at the outer enamel surface, and reduced cervically (also see Shellis, 1984), which has also been reported for macaque deciduous enamel (Smith et al., 2002). Birth is another temporary influence on

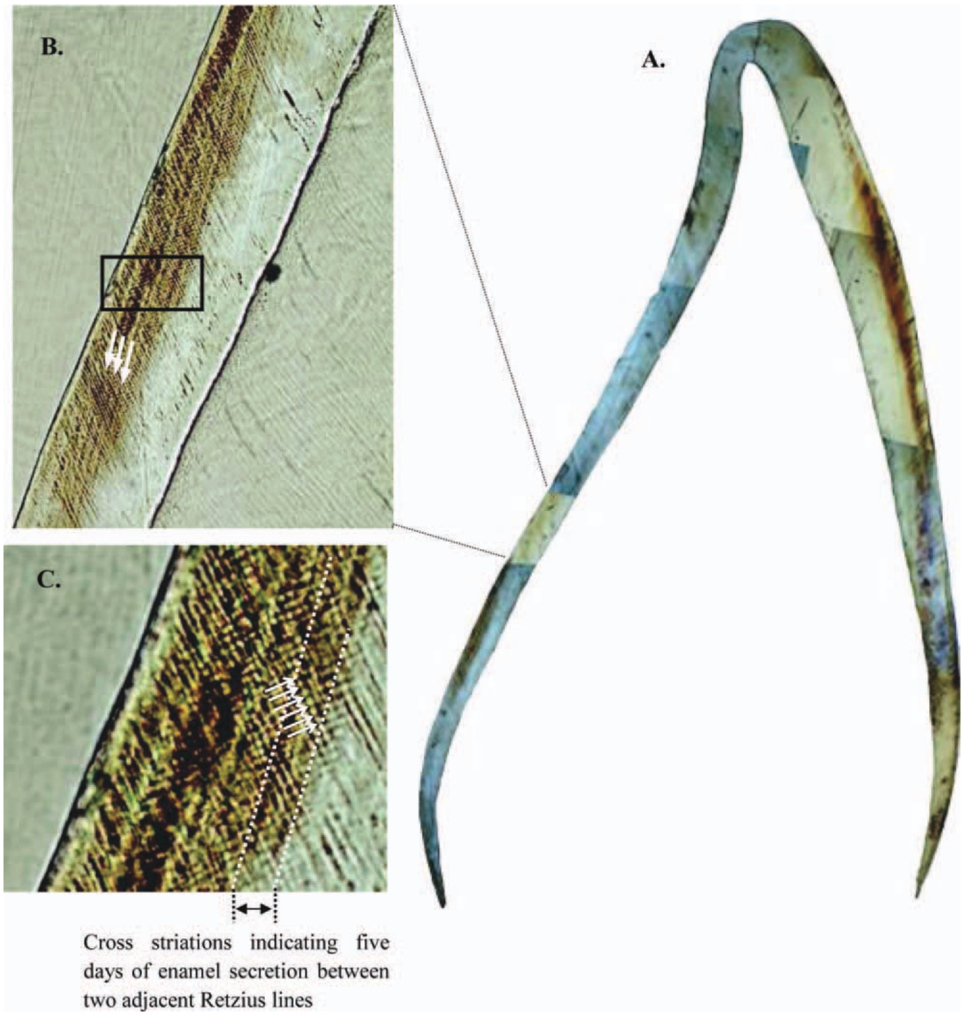

Fig. 1. Retzius line periodicity in di_2. **A**: Photomontage of a di_2 section taken at 4×. **B**: Lingual surface, lateral enamel at 10× showing Retzius lines (indicated by arrows). The darker area between the Retzius lines is hypomineralized enamel. **C**: Close up of highlighted area in B at 40× showing daily cross-striations between two adjacent Retzius lines. White-dashed lines follow Retzius lines axis. White arrows point to cross-striations.

deciduous DSRs (Macchiarelli et al., 2006; Birch and Dean, 2009; Mahoney, 2011). No study has examined DSR variation between maxillary and mandibular teeth, or between incisors and canines in samples sizes greater than $n = 1$.

Retzius and intradian line periodicity. A previous study of incremental markings reported a Retzius line periodicity range from 4 to 8 days within and between three deciduous teeth (Huda and Bowman, 1994). As they noted, it was not clear if the range of values within each tooth reflected a methodological limitation or actual variation (Huda and Bowman, 1995). Mahoney (2011) reported a periodicity of 9 days for one deciduous second molar. No study has reported Retzius line periodicity for deciduous incisors, or intradian line periodicity for human deciduous anterior enamel.

Crown formation time. Early estimates of deciduous CFT were attained from serial sections taken through the teeth and jaw of known age cadavers (Logan and Kronfeld, 1933). Following this, mean age of crown completion for deciduous anterior teeth (and molars) was calculated from radiographs taken of the developing den-

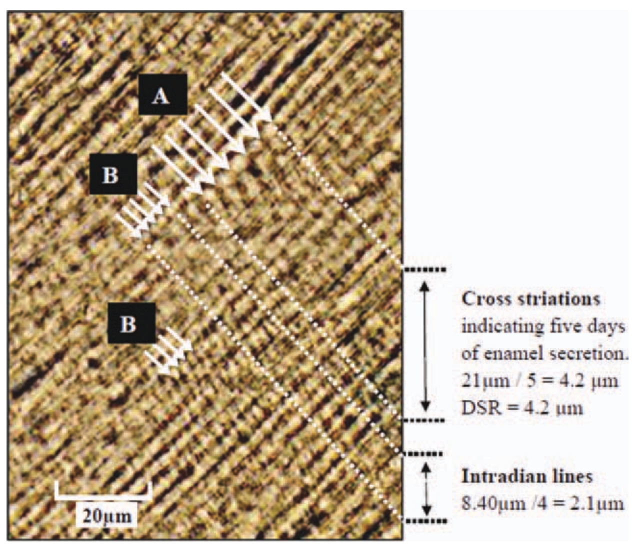

Fig. 2. Intradian lines in di_2 at 40×. **A**: Large white arrows point to daily cross-striations. **B**: Small white arrows point to intradian lines.

tition from children in three or six monthly intervals, over several years (e.g., Fanning, 1961; Moorrees et al., 1963; Fanning and Brown, 1971). Others supplemented radiographic examinations with tooth length measurements (Liversidge and Molleson, 2004).

Few have reported enamel CFT for deciduous anterior teeth from histological analyses of incremental markings. Shellis (1984) calculated CFTs for deciduous maxillary and mandibular lateral incisors ($n = 2$) and canines ($n = 4$) combined using a formula that quantified extension rates along the EDJ (though, see Discussion in Smith et al., 2006). Katzenberg et al. (2005) reported formation time for di^2 and dc^1, but as they noted, the enamel was damaged so it was difficult to provide an accurate CFT. FitzGerald et al. (1999, 2006) calculated a CFT of twelve months for six canines (mandibular and maxillary combined), 6 months for one lateral incisor, and 5 months for one central incisor.

CFTs derived from radiographic methods can differ when compared with those attained from histological analyses of incremental enamel markings (e.g., Beynon et al., 1991a,b, 1998b; Reid et al., 1998a,b; FitzGerald et al., 1999; Reid and Dean, 2006; Mahoney, 2011). Relatively reduced values reported in the radiographic studies have been attributed in part to the imaging technique (e.g., Beynon et al., 1991a). In contrast, CFT calculated from incremental markings can yield accurate (Smith et al., 2006; Antoine et al., 2009) and consistent estimates (FitzGerald and Hillson, 2009). Given that CFTs can contribute to modern human age-at-death estimates (e.g., Boyde, 1964b), and the general lack of histologically derived formation times for deciduous anterior teeth, this makes a case for undertaking this study on this aspect of dental development.

Pre- and postnatal cusp growth. Studies employing staining methods (Kraus, 1959b; Kraus and Jordan, 1965) report a sequence of deciduous enamel initiation: central incisors, followed by first molars, lateral incisors, canines, and lastly second molars. Others report initial calcification in di^2 compared with di_2 (Butler, 1992; Kraus, 1959b), though there is variation (Logan and Kronfeld, 1933).

Histological analyses of initial mineralization has been undertaken for deciduous dentin (Sunderland et al., 1987), incisor and canine enamel (FitzGerald and Hillson, 2009) and lower first and second molar enamel (FitzGerald and Hillson, 2009; Mahoney, 2011). Of these, Sunderland et al. (1987) reported a sequence of initiation along the deciduous tooth row:central incisors, followed by lateral incisors or first molars, then canines, and lastly second molars.

The aim of this study is to reconstruct incremental enamel development for a sample of modern human deciduous anterior teeth. The findings will be compared with deciduous molars to search for developmental differences along the tooth row. Links with the eruption sequence will also be sought.

MATERIALS

The dental sample is comprised of erupted unworn di_1($n = 13$), di_2($n = 12$), dc_1($n = 17$), and di^1($n = 11$), di^2($n = 14$), and dc^1($n = 17$). These were chosen from a much larger sample of sectioned deciduous anterior teeth because they preserved either incremental and/or accentuated markings. All dental samples dated to the British Medieval period and were from a previously excavated archaeological site, St Gregory's Priory and adjacent cemetery, in Canterbury, England (Hicks and Hicks, 2000). Samples were chosen from this site because of the large number of well-preserved infants and juveniles. The sex of the juveniles was not known.

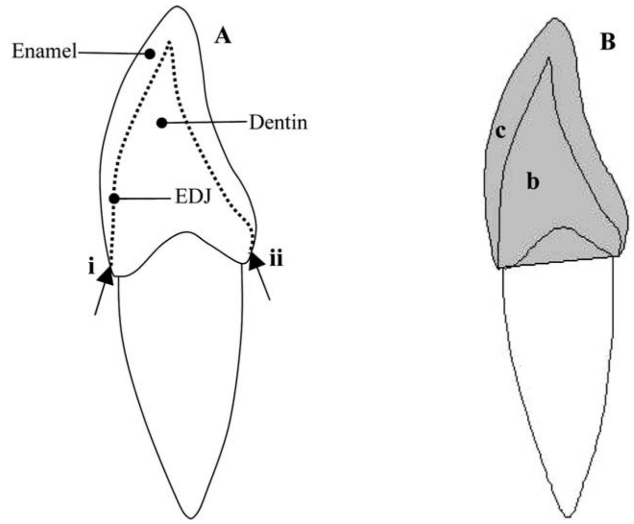

Fig. 3. Measurements (from Martin, 1983) for estimating CFT from regression equations. **A**: Total length of the EDJ in millimeters measured between (i) and (ii). **B**: Total area of the tooth crown section in square millimeter (highlighted area). This is the area of the enamel cap (c), plus the dentin area (b) defined by a line drawn between the most cervical tip of the enamel labial face across to the most cervical tip of the lingual face.

METHODS

Standard histological procedures were followed (e.g., Reid et al., 1998a). Each tooth was embedded in polyester resin to reduce the risk of splintering while sectioning. Using a diamond-wafering blade (Buehler® IsoMet 1000), labial-lingual sections were taken through the outermost enamel cusp tip, the tip of the EDJ, and the most cervical extension of the enamel. Section obliquity was minimized following methods discussed by Mahoney (2010). Each section was mounted on a microscope slide, lapped using a graded series of grinding pads (Buehler® IsoMet 1000) to reveal the accentuated and other incremental lines, polished with a 0.3-mm aluminum oxide powder, placed in an ultrasonic bath to remove surface debris, dehydrated through a series of alcohol baths, cleared (Histoclear®), and mounted with a cover slip using a xylene-based mounting medium (DPX®). Sections were examined under a high powered microscope (Olympus BX51) using transmitted and polarized light. Images were captured (Olympus DP25) and analyzed (Olympus Cell D). The timing of enamel development was reconstructed (below).

Daily enamel secretion rates

DSRs were calculated for cuspal, lateral, and cervical enamel areas (see Beynon et al., 1991a, their Fig. 2). Each area was further subdivided into three regions of equal thickness (inner, mid, and outer). Rates were measured along the long axis of an enamel prism around the center of each region (Mahoney, 2008: Fig. 3). A distance corresponding to 5 days of enamel secretion was measured, and then divided by five to yield a mean daily rate. The procedure was repeated a minimum of six times in each region, which allowed a grand mean value and standard deviation (SD) to be calculated.

Retzius line periodicity

Retzius lines were only visible in the lateral enamel of six sections from the entire anterior tooth sample. Periodicity for one of these sections was calculated by directly counting the number of cross-striations between two adjacent Retzius lines to give the number of days of enamel formation across a single enamel layer (see Fig. 1). Periodicity for the other sections was calculated by measuring the distance between several adjacent Retzius lines along the long axis of the prism. The measurement was divided by a local DSR.

To supplement the comparative molar data (Mahoney, 2011), and to assess variation in Retzius line periodicity in teeth from the same jaw, the mandibles that contained the six anterior teeth that preserved Retzius lines were re-sampled for deciduous first and second molars. Multiple sections were taken through each tooth. In one jaw containing anterior teeth, Retzius lines were present in one deciduous mandibular first molar and periodicity was calculated. In another jaw not containing anterior teeth, Retzius lines were present in one permanent first molar and a deciduous second molar and periodicity was calculated.

Intradian line periodicity

Intradian lines were visible in the cuspal enamel of three sections from the entire sample. For one of these sections, cross-striations were adjacent to intradian lines (see Fig. 2). For this section, periodicity was determined by measuring the distance across four intradian lines along the long axis of a prism, which was then subdivided to calculate the rate of enamel secretion between two lines. The procedure was repeated across three intradian lines in another area on the same slide and a mean value was produced. The amount of enamel secreted between two intradian lines was then compared with the amount of enamel secreted over a 24-h period (i.e., between two adjacent cross-striations on the same thin section) to calculate intradian line periodicity.

Cuspal enamel formation time

For one of the deciduous lateral incisors and two canines, cuspal formation time was calculated for both the labial and lingual surfaces. For all other teeth, formation time was calculated for just the labial surface. Cuspal enamel formation time was calculated in two ways. In five sections, cross-striations were preserved throughout most of the cuspal enamel. For these sections, overlapping images of the entire sectioned cuspal enamel were produced at 20× using imaging software. These were printed in color and a montage was recreated. Cross-striations on the montage were marked with a pen, starting at the tip of the dentin horn and continuing to the outer enamel surface at the cusp tip. The number of cross-striations was then summed to give the number of days of cuspal enamel growth.

For the remaining and majority of the sections, cross-striations were preserved intermittently. For these, formation times were calculated using a standard formula [(enamel thickness × correction factor)/DSR]. Enamel thickness was measured from the tip of the dentin horn to the position of the first Retzius line at the cusp tip tooth surface. A correction factor of 1.05 was used because decussation was not marked in this sample (e.g., Schwartz et al., 2003). Cuspal enamel was divided into three regions of equal thickness and divided by the mean DSR from each of those regions (see above). The three formation times were then summed to give an overall cuspal formation time.

Lateral enamel formation time

Lateral enamel formation time was recorded using enamel prism lengths divided by local mean DSRs to navigate between accentuated markings (Mahoney et al., 2007: his Fig. 1). Overlapping images of the entire lateral enamel were captured at 20× for each section and printed in color. A montage was created. Accentuated markings upon the montage were traced with a pen, so that they were clearly emphasized. The tracing was used as a template to guide recording of another on-screen image of the lateral enamel using the imaging software. A clearly visible accentuated marking in the lateral enamel was followed on-screen in an apical direction to the EDJ. Prisms originating at the boundary between the EDJ and this accentuated marking were traced toward another accentuated marking at or near the outer enamel surface. The procedure was repeated. The time taken to form these prisms was included in the estimate of lateral enamel formation time.

Crown formation time

Cuspal and lateral enamel formation times were summed for each tooth to give total CFT.

Pre- and postnatal cusp growth

Prenatal enamel cusp formation time was calculated by locating the position of the neonatal line. The enamel thickness between this line and the tip of the dentin horn was measured and divided into three regions of equal thickness. Each region was divided by a mean DSR calculated for each region. The three formation times were then summed to give prenatal cusp formation time.

The sequence of enamel cusp initiation and completion between teeth was determined by locating the position of the neonatal line and the position of subsequent accentuated markings. The time that elapsed between the neonatal line and the subsequent markings was calculated by dividing the enamel thickness by local DSRs, thus determining a chronology of growth disturbances. The chronology of disturbances was then sought in and matched between the tooth types.

Analysis

DSRs from equivalent regions will be compared between anterior tooth types, between mandibular and maxillary anterior teeth, and between anterior and posterior mandibular teeth with a Mann–Whitney *U*-test. A Wilcoxon signed-rank test will be used to compare DSRs from anterior teeth, between cuspal and lateral enamel. Variation in maxillary and mandibular anterior CFTs will also be sought with a Wilcoxon signed-rank test.

TABLE 1. Mandibular anterior tooth enamel DSRs in micrometers per day

	di_1			di_2			dc_1		
	Inner (n = 8)	Mid (n = 13)	Outer (n = 7)	Inner (n = 12)	Mid (n = 11)	Outer (n = 8)	Inner (n = 15)	Mid (n = 13)	Outer (n = 8)
Cuspal enamel									
Mean	3.68	4.50	5.16	3.35	4.60	5.14	3.31	4.09	4.79
Min	2.44	3.74	4.83	2.56	4.07	4.54	2.05	2.87	3.95
Max	4.50	5.25	5.63	3.90	5.60	5.71	3.80	4.90	5.31
± 1 SD	0.63	0.67	0.30	0.45	0.43	0.61	0.49	0.64	0.48
	Inner (n = 5)	Mid (n = 6)	Outer (n = 6)	Inner (n = 7)	Mid (n = 9)	Outer (n = 5)	Inner (n = 5)	Mid (n = 13)	Outer (n = 8)
Lateral enamel									
Mean	3.67	3.89	5.06	3.45	4.27	5.04	3.10	3.91	5.07
Min	3.43	2.97	4.73	2.91	3.36	4.68	2.50	2.87	4.61
Max	3.90	4.34	5.56	4.10	4.88	5.17	3.51	4.31	5.39
± 1 SD	0.29	0.61	0.36	0.43	0.47	0.25	0.58	0.37	0.34

Mean cervical DSRs for the mid-enamel region in di_2 = 3.42 μm (n = 4), and dc_1 = 3.52 μm (n = 3).

TABLE 2. Maxillary anterior tooth enamel DSRs in micrometers per day[1]

	di^1			di^2			dc^1		
	Inner (n = 11)	Mid (n = 9)	Outer (n = 5)	Inner (n = 14)	Mid (n = 9)	Outer (n = 7)	Inner (n = 10)	Mid (n = 7)	Outer (n = 6)
Cuspal enamel									
Mean	3.65	4.76	4.96	3.65	4.38	4.98	3.72	3.85	4.39
Min	2.00	4.06	3.91	2.06	3.40	3.70	2.88	2.67	3.44
Max	4.37	4.97	5.52	4.51	4.99	5.37	4.20	4.35	5.02
± 1 SD	0.71	0.46	0.63	0.69	0.71	0.59	0.37	0.52	0.62
	Inner (n = 5)	Mid (n = 6)	Outer (n = 2)	Inner (n = 9)	Mid (n = 6)	Outer (n = 6)	Inner (n = 7)	Mid (n = 15)	Outer (n = 6)
Lateral enamel									
Mean	3.37	3.96	4.31	3.46	3.64	4.26	3.83	4.07	4.62
Min	2.78	3.06	–	2.44	3.27	3.48	2.89	3.01	3.94
Max	3.76	4.30	–	4.50	3.98	4.80	4.03	4.91	5.20
± 1 SD	0.45	0.53	–	0.70	0.34	0.44	0.45	0.51	0.55

Mean cervical DSRs for the dc^1 = inner 3.10 μm (n = 2), mid 3.57 μm (n = 6), outer 3.93 μm (n = 3). Mean cervical DSRs for the di^2 = mid 3.29 μm (n = 2). Mean cervical DSRs for the di^1 = inner 3.10 μm (n = 3), mid 3.27 μm (n = 4), outer 3.83 μm (n = 2).

Data normality will be checked with a one sample Kolmogorov–Smirnov test.

RESULTS

Anterior teeth

Daily enamel secretion rates. Mean DSRs increased from inner to outer enamel regions in all tooth types (Tables 1 and 2). DSRs did not differ significantly when equivalent regions were compared between anterior tooth types, or between mandibular or maxillary teeth, except when the canine inner cuspal regions were compared. Mean DSRs were generally slightly faster in cuspal compared with lateral enamel, though the difference was only significant in di^1 (Appendix 1 for anterior tooth inferential statistics). When DSRs could be calculated for cervical enamel they were, on average, between 1.08 and 0.38 μm slower than equivalent regions in cuspal enamel, which supports results reported by Birch and Dean (2009).

Retzius line periodicity. In mandibular anterior teeth, periodicity was calculated for one lateral incisor and two canines. Direct counts of cross-striations between two adjacent Retzius lines gave a periodicity of 5 days for the incisor (see Fig. 1a–c). A measurement of 63 μm across four Retzius lines (i.e., three layers) divided by a local DSR of 3.81 μm gave a measurement of 5.51, or a periodicity of 6 days for one canine. Measurements of 89 μm across four layers divided by a local DSR of 4.00 μm, and another measurement of 120 μm across five layers divided by a DSR of 4.2 μm, gave two values of 5.56 and 5.71, respectively, or a periodicity of 6 days for this canine.

In maxillary anterior teeth, periodicity was calculated for three canines. Measurements of 59 μm across two enamel layers divided by a DSR of 5.01 μm, another of 51 μm across two layers divided by a DSR of 5.00 μm, and another of 137 μm across six layers divided by a DSR of 4.80 μm gave a periodicity of 6 days for the first canine, and 5 days for the other two canines.

Intradian line periodicity. Intradian line periodicity was 2.1 μm and 2.0 μm in one di_2 section, with a DSR of 4.2 μm calculated from adjacent daily cross-striations in the same section (see Fig. 2). Based upon a 24-h periodicity for the cross-striations used to calculate the DSR of 4.2 μm, the intradian lines were laid down every 12 h. The 12-h intradian periodicity calculated for this slide is the same as the 12-h intradian periodicity reported for human permanent dentin (Kawasaki et al., 1979).

TABLE 3. Incisor and canine formation times in days (years)

	Mandibular				Maxillary			
	di$_2$ (n = 11)		dc$_1$ (n = 17)		di^2 (n = 12)		dc^1 (n = 17)	
	Cu[a]	Lat	Cu	Lat	Cu	Lat	Cu	Lat
	53	270	44	325	49	218	101	423
	40	266[b]	87	430	64	282	91	479
	43	229	79	321	69	291	76	378
	74	307	73	369	59	236	113	331
	56	209	87	296	54	244	103	386
	59	228	95	361	60	–	97	350[c]
	50	269	98	297	46	289	86	321
	67	268	68	312	44	339	97	336
	38	332	55	331	94	295	65	358
	46	270	73	–	46	362	76	331
			77	333	47	320	135	426
			90	416			140	377
			84	408			89	354
			112	410			99	374
			72	459			51	434
			68	414			64	444
			81	353			88	–
CFT[c]	317 (0.87)		443 (1.21)		345 (0.95)		474 (1.30)	
Min	265		369		267		407	
Max	381		531		408		570	
± 1 SD[d]	38		57		45		51	

di$_1$ (n = 3) mean cuspal of 42 days + lateral of 240 days = CFT of 282 days; di^1 (n = 3) mean cuspal of 69 days + lateral of 319 days = CFT of 388 days.
[a]Cu = cuspal enamel; Lat = lateral enamel.
[b]Labial face reported in table, but lingual face also reported in results.
[c]Total mean CFT and SD in table calculated from individuals with both cu + lat.

TABLE 4. Prenatal formation times in days

	di$_1$	di$_2$	dc$_1$	di^1	di^2	dc^1
	181	130	92	201	104	77
	174	118	77	188	90	92
	146	84	75	169	170	103
	162	139	75	199	180	89
		162	101		196	127
		125	60		216	76
		168	74		186	90
		188	91			97
		169	110			89
			107			113
			118			132
			84			88
			90			
$\bar{X}$	166	142	88	189	163	98

Crown formation time. Mean CFT was 282 days for di$_1$, 317 days for di$_2$, and 443 days for dc$_1$. When CFT was calculated for both faces of one di$_2$, it gave a formation time of 306 days for the labial face and 279 days for the lingual face. Table 3 shows lateral and cuspal formation times.

Mean CFT for di^1 was 388 days, 345 days for di^2, and 474 days for dc^1. When CFT was calculated for both faces of two canines it gave a formation time of 447 days for the labial face and 402 days for the lingual face of one canine, and 473 days for the labial face and 424 days for the lingual face of the other. Mean CFTs for di^2 and dc^1 were slightly greater compared with di$_2$ and dc$_1$, but formation times did not differ significantly between the mandibular and maxillary antimeres.

CFT was significantly correlated with the total area of the tooth crown section (Pearson's r = 0.758; P = 0.000), and the length of the EDJ (Pearson's r = 0.712; P = 0.000; Fig. 3a,b). Thus, linear regression equations were calculated (data from all anterior teeth combined). These can be applied to incisors (or canines) with unworn enamel and those where the occlusal enamel is worn but the EDJ remains intact. To estimate CFT for unworn incisors: di1 CFT = 122.980 + (11.357 × area of tooth crown section). To estimate CFT for worn incisors: di1 CFT = −236.268 + (43.751 × length of EDJ).

Pre- and postnatal cusp growth. In mandibular teeth, on average, enamel initiated 166 days before birth in di$_1$, 142 days before birth in di$_2$, and 88 days before birth in dc$_1$ (Table 4). Enamel was complete 116 days after birth in di$_1$, 175 days after birth in di$_2$, and 355 days after birth in dc$_1$. Growth continued for an additional 180 days in dc$_1$ after enamel completion in di$_2$.

In maxillary teeth, on average, enamel initiated 189 days before birth in di^1, 163 days before birth in di^2, and 98 days before birth in dc^1 (Table 4). Enamel was complete 199 days after birth in di^1, 182 days after birth in di^2, and 376 days after birth in dc^1. The neonatal line formed over a period of 3–7 days in all teeth, mandibular and maxillary.

Figures 4 and 5 show di$_2$ and dc$_1$ CFT re-calculated as pre- and postnatal formation times. Figures 6 and 7 show di^2 and dc^1 CFT re-calculated as pre- and postnatal formation times. Mean postnatal formation time for maxillary and mandibular lateral incisors and canines were greater compared with formation times derived from radiographic methods (Table 5), which supports previously documented differences in CFT between the two methodologies (e.g., Beynon et al., 1991a).

Comparisons along the tooth row

Daily enamel secretion rates. Mean mandibular cuspal DSRs for di$_1$ (mid = 4.50 μm, outer = 5.16 μm) and di$_2$ (mid = 4.60 μm, outer = 5.14 μm) were slightly

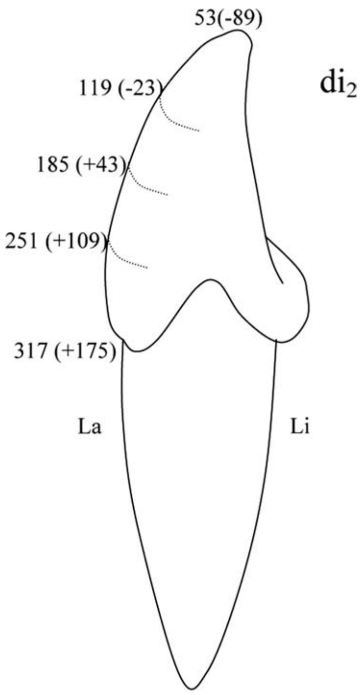

Fig. 4. Deciduous mandibular lateral incisor enamel CFT. The figure shows mean enamel formation time for di_2 subdivided into quartiles, which are indicated by lines and days of occurrence, with the corresponding pre (−) and postnatal (+) chronological age in days given in parenthesis. Values show that 89 days before birth, cuspal enamel is complete. Lateral enamel growth continues and crown formation is complete 175 days after birth. La = Labial. Li = Lingual. Values were taken from Tables 3 and 4 and re-calculated.

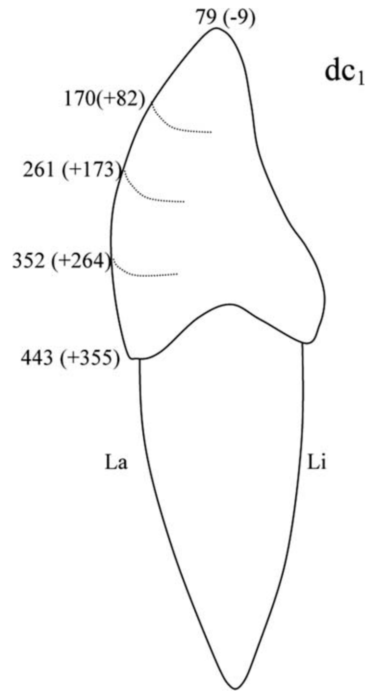

Fig. 5. Deciduous mandibular canine enamel CFT. The figure shows mean enamel formation time for dc_1 subdivided into quartiles, which are indicated by lines and days of occurrence, with the corresponding pre (−) and postnatal (+) chronological age in days given in parenthesis. Values show that 9 days before birth, cuspal enamel has formed. Lateral enamel growth continues, and crown formation is complete 355 days after birth. La = Labial. Li = Lingual. Values were taken from Tables 3 and 4 and re-calculated.

greater compared with equivalent regions in dm_1 (mid = 3.87 μm, outer = 4.76 μm; Mahoney, 2011, his Tables 1 and 3) and dm_2 (mid = 3.91 μm, outer = 4.92 μm; see Fig. 8). DSRs differed significantly between di_2 and dm_2 midenamel regions (U = 5.000; Z = −3.411; P = 0.001), but not when DSRs from other regions were compared between anterior and posterior teeth.

Retzius line periodicity. Retzius lines were present in one deciduous mandibular first molar and periodicity was calculated. A measurement of 56.93 μm across three enamel layers divided by a local DSR of 3.56 μm gave a figure of 5.33 or a periodicity of 5 days. The periodicity of the lateral incisor from the same mandible calculated from direct counts of cross-striations was 5 days (see Fig. 1). The lateral incisor periodicity was recalculated in another area of the enamel from a prism length divided by a local DSR. A measurement of 38.40 μm across two layers divided by a local DSR of 4.18 μm (16.73 μm/4) gave a figure of 4.59, or a periodicity of 5 days.

Retzius lines were present in one permanent first molar and a deciduous second molar from the same jaw. Measurements of 120.00 μm across three enamel layers in one section from the permanent molar, divided by a local DSR of 5.40 μm gave a figure of 7.40 or a periodicity of 7 days. Measurements of 143.00 μm across four enamel layers in another section from the same molar divided by a DSR of 5.00 μm gave a figure of 7.15 or a periodicity of 7 days. A measurement of 55.00 μm across two layers in a section from the deciduous second molar divided by a local DSR of 3.87 μm gave a figure of 7.10, or a periodicity of 7 days.

Pre- and postnatal cusp growth. When mandibular anterior tooth enamel initiation times are compared with initiation times previously reported for deciduous mandibular molars (Mahoney, 2011), a chronology of initial enamel growth can be reconstructed along the tooth row. The di_1 initiates first, then di_2, dm_1, dc_1, and lastly dm_2 (Fig. 9).

DISCUSSION

Daily enamel secretion rates

Deciduous mandibular incisors and molars have slightly different growth trajectories (Fig. 8). A greater quantity of enamel is secreted each day in the midincisor enamel region, compared with the same region in molars. Mean DSRs are also slightly elevated in outer incisor enamel compared with molars. This differs from human permanent teeth, which showed limited DSR variation between some tooth types (Beynon et al., 1991b).

Some of the DSR variation along the deciduous tooth row could be due to the neonatal line. Enamel secretion rates can be temporarily reduced immediately after birth compared with before (Macchiarelli et al., 2006; Birch and Dean, 2009; Mahoney, 2011). A neonatal line is present in deciduous molar cuspal enamel (midenamel regions in dm_1 hypoconid and entoconid, and dm_2 metaconid; dm_2 protoconid outer region; Mahoney, 2011: compare his Tables 5–8). Since this line is usually not present in incisor cuspal enamel (compare Table 3 with

4), birth might explain some of the DSR variation between molars and incisors. However, birth is unlikely to have had an effect on either dc_1 or dc^1 cuspal DSRs, as the average period of canine cuspal enamel growth is approximately equivalent to the average period of prenatal enamel growth (see methodological findings below). Nevertheless, mean DSRs from canine cuspal mid and outer enamel regions are also slightly reduced compared with incisors (Tables 1 and 2). Neither does dm_2 hypoconid and entoconid inner cuspal enamel contain a neonatal line. Nevertheless, mean DSRs from inner enamel in this tooth type, along with all other deciduous tooth types, are still greater compared with permanent molar inner enamel (Fig. 10). Therefore, some, but not all of the DSR variation between the tooth types can be explained by birth (see Discussion in pre- and postnatal cusp growth section below). Overall, mean cuspal DSRs were fastest in deciduous incisors, slowed along the tooth row in deciduous molars, and were slowest in permanent molars, depending on which region of the tooth was compared.

Retzius line periodicity

Retzius line periodicity in the anterior teeth ranged between 5 and 6 days. When combined with the values of 7 and 9 days calculated for two deciduous molars (see Results section, and Mahoney, 2011) this gives a range from 5 to 9 days. The lowermost value of 5 days is less

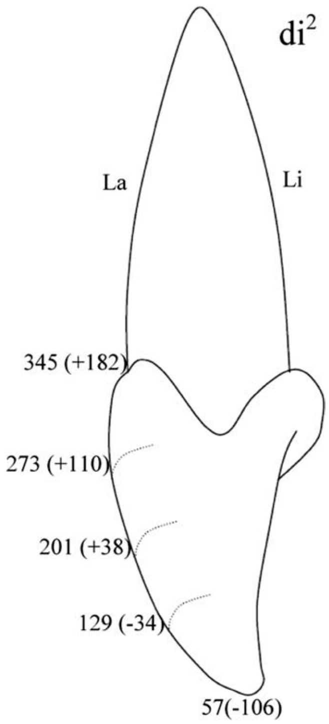

Fig. 6. Deciduous maxillary lateral incisor enamel CFT. The figure shows mean enamel formation time for di^2 subdivided into quartiles, which are indicated by lines and days of occurrence, with the corresponding pre (−) and postnatal (+) chronological age in days given in parenthesis. Values show that 106 days before birth, cuspal enamel is complete. Lateral enamel growth continues and crown formation is complete 182 days after birth. La = Labial. Li = Lingual. Values were taken from Tables 3 and 4 and re-calculated.

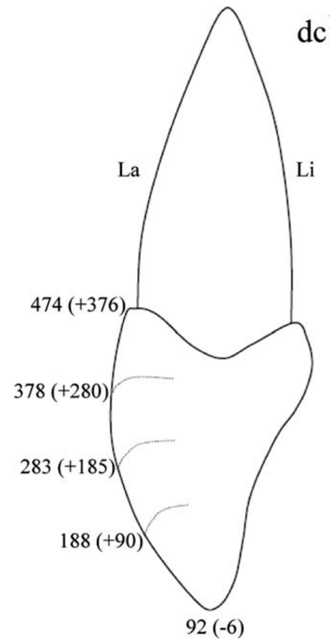

Fig. 7. Deciduous maxillary canine enamel CFT. The figure shows mean enamel formation time for dc^1 subdivided into quartiles, which are indicated by lines and days of occurrence, with the corresponding postnatal chronological age in days given in parenthesis. Values show that 6 days before birth, cuspal enamel is complete. Lateral enamel growth continues, and crown formation is complete 376 days after birth. La = Labial. Li = Lingual. Values were taken from Tables 3 and 4 and re-calculated.

TABLE 5. Comparing deciduous incisor and canine mean CFT (± 1 SD) in years after birth

di_2	dc_1	di^2	dc^1	Authors
–	0.65 (0.54–0.79)	–	–	Fanning (1961)[a]
–	0.70 (0.60–0.80)	–	–	Moorrees et al. (1963)[b]
0.25	0.75	0.20	0.75	Nomata (1964)
–	0.77 (0.56–1.07)	–	–	Fanning and Brown (1971)[c]
0.32 (0.25–0.39)	0.81 (0.69–0.93)	0.28 (0.04–0.52)	0.83 (0.57–1.09)	Liversidge and Molleson (2004)[d]
0.48 (0.37–0.58)	0.97 (0.82–1.13)	0.50 (0.38–0.62)	1.03 (0.89–1.17)	This study[e]

[a] 50th, 25th, and 75th mean percentiles calculated from males and females.
[b] Calculated from figure in publication.
[c] 3rd, 50th, and 97th percentiles calculated from males and females.
[d] Mean age of attainment for enamel crown completion.
[e] This study. Re-calculated from Tables 3 and 4. Mean postnatal formation times for di^1 of 0.51 years (n = 3) and 0.32 years for di_1 (n = 3) are also greater than mean age of attainment reported by radiographic methods: di^1 = 0.12 years; dc_1 = 0.10 years (Liversidge and Molleson, 2004).

than the lowermost value of 6 days reported for modern human permanent teeth (e.g., Reid and Ferrell, 2006; Mahoney, 2008). Therefore, at first glance, the results reported here do not appear to support the hypothesis that the range of Retzius line periodicities in deciduous teeth will be the same as in permanent teeth. However, periodicity remained constant between a deciduous and permanent molar from the same jaw, which does not suggest that these different tooth types have different ranges. If this is confirmed, then the lowermost value reported here extends the known range for modern humans. Future studies can assess this proposal with larger data sets. Retzius line periodicity also remained constant when calculated in two different enamel regions in one lateral incisor (see Results), which does not support the idea that periodicity varies within a deciduous tooth (Huda and Bowman, 1995).

Retzius line periodicity remained constant between a deciduous incisor and deciduous molar from one jaw. This finding is the same as the results reported for human permanent teeth, where periodicity also remains constant between teeth from the same jaw (e.g., Dean and Beynon, 1991; FitzGerald, 1998; Reid et al., 1998a).

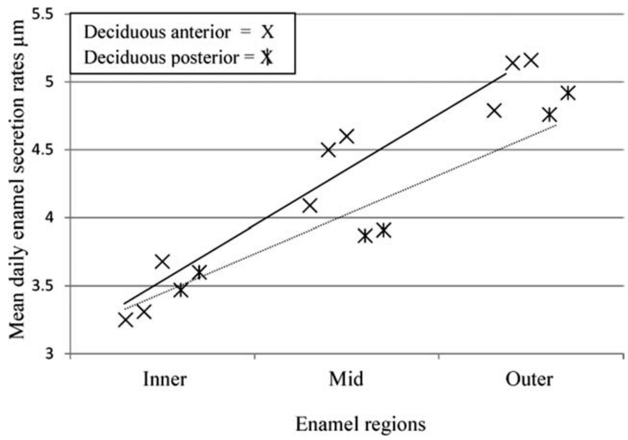

Fig. 8. Mean cuspal DSRs for deciduous mandibular anterior and posterior teeth. X = mean cuspal DSRs for mandibular di_1, di_2, and dic_1 taken from Table 1. X = mean cuspal DSR for mandibular dm_1 and dm_2, taken from Mahoney (2011).

Deciduous incremental enamel development and tooth eruption

Beynon et al. (1991a) proposed that aspects of incremental development in permanent teeth from a juvenile gorilla reflected mean tooth emergence times. Several of the results presented here suggest that this also applies to modern human deciduous teeth. First, clinical longitudinal studies of living children (Lysell et al., 1962; Roche et al., 1964; Hitchcock et al., 1984; Holman and Yamaguchi, 2005; Folayan et al., 2007; Woodroffe et al., 2010) report the mean deciduous eruption (emergence through the gingiva) sequence for mandibular and maxillary teeth: di1, di2, dm1, dc1, and dm2. This eruption sequence is the same as the mandibular enamel initiation sequence reported here (Fig. 9). Even if the previously noted variation in di2 and dm1 initiation is accounted for, there are still some similarities between eruption and initiation of the earliest (di1) and latest (dc1, dm2) forming teeth.

In addition to enamel initiation times, other links between deciduous incremental enamel development and the eruption sequence are apparent. Relative to the

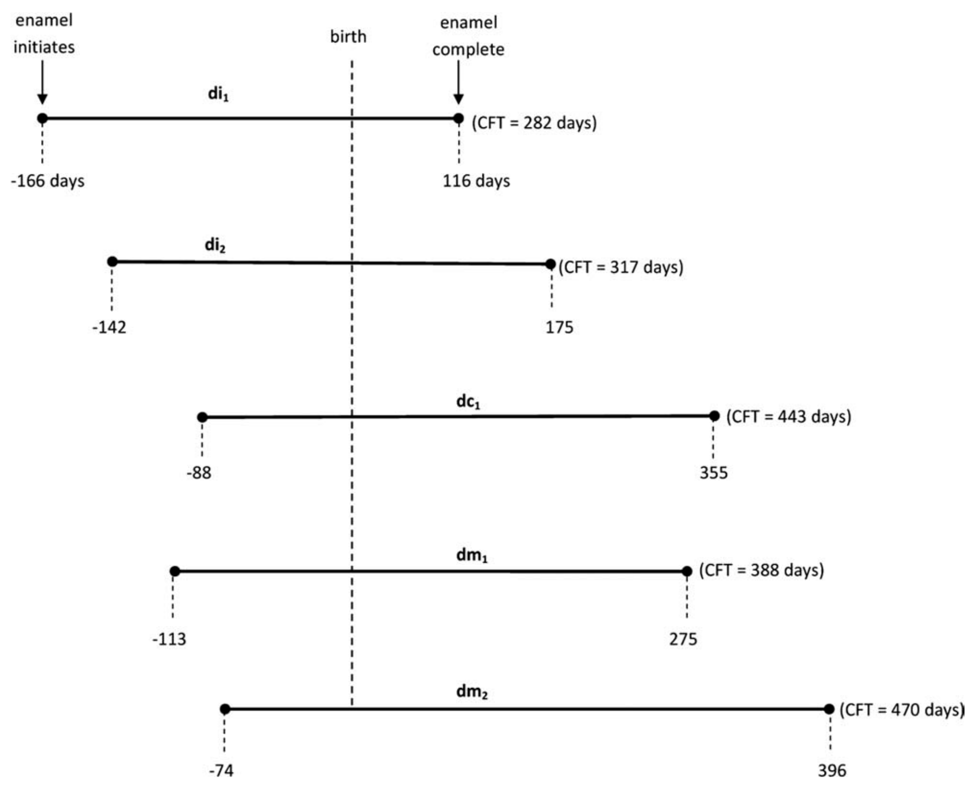

Fig. 9. Cusp initiation and completion times for deciduous mandibular teeth. Data for di_1, di_2, and dc_1 taken from Tables 3 and 4. Data for dm_1 protoconid, and dm_2 protoconid and hypoconid combined taken from Mahoney (2011).

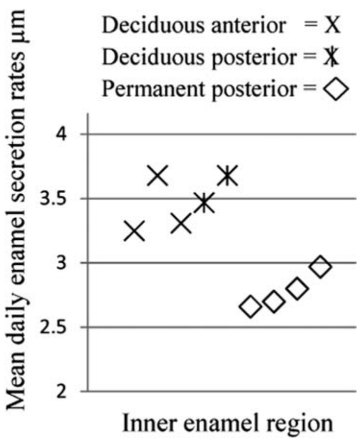

Fig. 10. Mean inner enamel cuspal DSRs. ✳ = mean cuspal DSR for mandibular di_1, di_2, and dic_1 taken from Table 1. ◇ = mean cuspal DSR for mandibular dm_1 and dm_2, taken from Mahoney (2011). Mean DSR for permanent molars taken from Dean (1998), Beynon et al., (1991), Lacruz and Bromage (2006), Reid et al. (1998), and Mahoney (2008; and see his Table 8 for calculations).

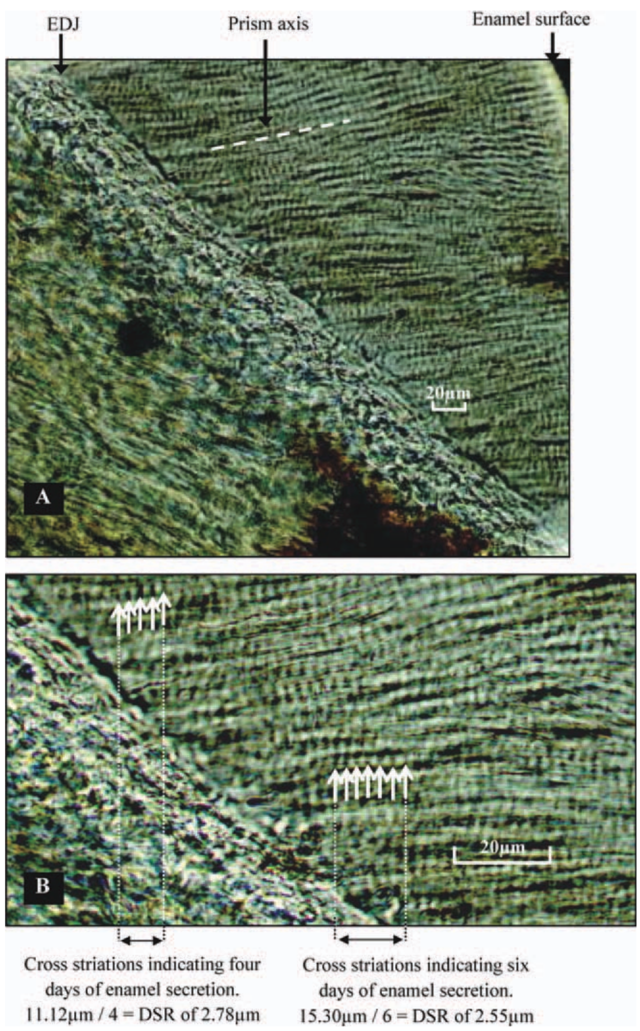

Fig. 11. Cross-striations adjacent to the EDJ in dc^1. **A**: 10×. **B**: Close up of A at 40×.

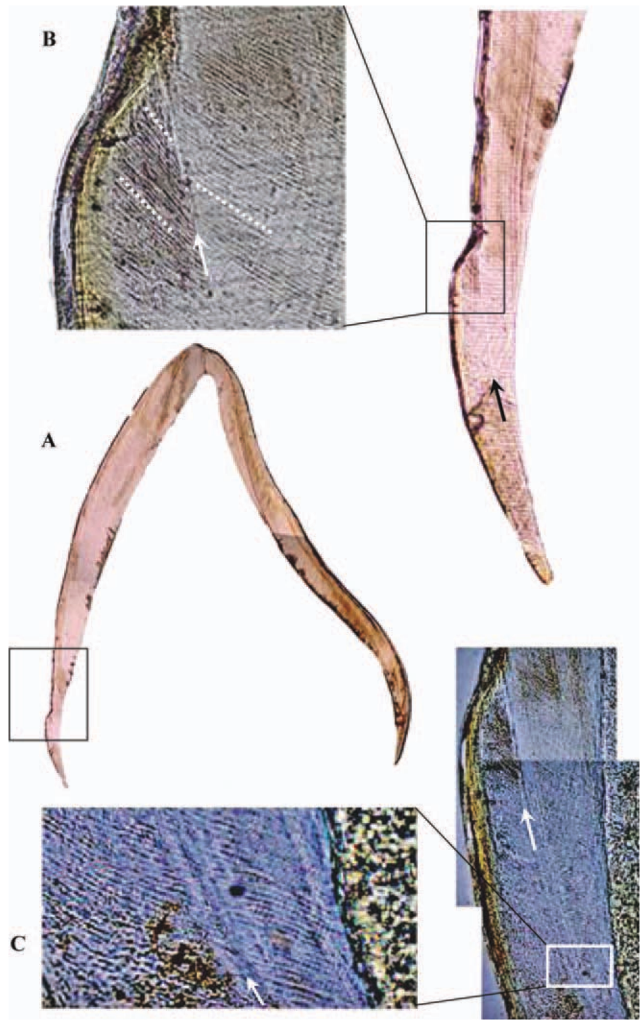

Fig. 12. Accentuated marking and surface hypoplasia in dc^1. **A**: Montage of dc^1 at 4×. **B**: Close up at 20× of hypoplastic defect. White arrow points to accentuated marking that emerges at outer enamel surface as a type of hypoplasia. Dashed white lines trace the change in prism axis, before and after the accentuated marking. **C**: Close up at 40× showing the change in the visibility of cross-striations, before and after the accentuated marking. White arrow points to accentuated marking, EDJ is to the right.

other tooth types along the deciduous mandibular tooth row, incisor enamel had the fastest mean DSRs (mid- and outer regions), the greatest proportion of prenatal formation time (maximum of 59%, minimum of 45%: Tables 3 and 4), the shortest postnatal formation time, but is amongst the first tooth type to erupt (based upon the clinical studies). Thus, the incremental development of mandibular incisor enamel suggests links with the eruption sequence. If this is accepted, then the relatively advanced development in the incisors, and accelerated DSRs that cannot be explained by birth, makes sense, as this is likely tied to the need to develop this tooth rapidly as it is the first human tooth to erupt.

If links between deciduous incremental enamel development and eruption prove consistent in future studies, then this might provide one alternative way of evaluating eruption sequences for deciduous teeth that have completed development but are recovered outside of the jaw. For example, by reconstructing a chronology of dental development using the neonatal line, or other accentuated markings, to register development between teeth from one individual, it might then be possible to reconstruct the eruption sequence and potential life history events. Future studies may test this proposal for applicability in studies of non-human primates (e.g., Smith et al., 1994; Godfrey et al., 2004).

Methodological findings

Cross-striation and prism visibility within deciduous anterior teeth are dependent on the region of the enamel examined. Cross-striations and prisms were usually visible in cuspal and lateral inner enamel of all tooth types. Consequently, DSRs could generally be calculated for this region, even directly adjacent to the EDJ (see Fig. 11). This suggests that the structure-less layer (up to 15 μm) of enamel adjacent to the EDJ in permanent teeth (Osborn, 1973) can be narrower in deciduous teeth. Cross-striations and prisms were relatively less visible in the outermost enamel (e.g., Ripa, 1966, Gwinnett, 1966). Cross-striations were least visible in the cervical enamel of all teeth studied. In addition to the region examined, cross-striation visibility (and prism orientation) was influenced by an accentuated marking that emerged at the outer surface as a type of hypoplasia (Fig. 12a–c).

Accentuated markings were rarely preserved in central incisors, especially mandibular incisors, thus CFT could only be calculated for six individuals for this tooth type (Table 3: footnote 3). An alternative method for estimating CFT in central incisors is from linear regression equations (see Results).

CONCLUSION

This study reconstructed incremental enamel development in a sample of modern human deciduous maxillary and mandibular anterior teeth. Results were compared with deciduous molars to test the hypotheses that Retzius line periodicity and DSRs remained constant along the tooth row, as in permanent teeth. Links between incremental development and the deciduous eruption sequence were also sought. It was found that Retzius line periodicity remained constant along the deciduous tooth row, though the lower most values reported here for deciduous teeth are less than those previously reported by the majority of previous studies on human permanent teeth. DSRs in mandibular incisors were slightly accelerated when compared with equivalent regions in mandibular molars. Birth may explain some, but not all of this variation. Instead, relatively rapid development in incisors in advance of early eruption may account for some of the variation in enamel secretion rates along the tooth row that cannot be explained by birth. If such links between incremental enamel development and the eruption sequence are also present in other primate deciduous dentition, then this might have applicability in studies of life history.

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APPENDIX

TABLE A1. Comparing mandibular anterior tooth enamel DSRs between tooth types

	U	*Z*	*P*	*U*	*Z*	*P*
	Cuspal inner region			Lateral inner region		
di1 vs. di2	26.000	−1.355	0.176	14.500	−0.093	0.926
di1 vs. dc1	26.000	−1.355	0.196	6.500	−2.089	0.075
di2 vs. dc1	72.000	0.000	1.000	8.500	−1.203	0.229
	Cuspal mid region			Lateral mid region		
di1 vs. di2	12.000	−2.537	0.219	10.500	−1.143	0.253
di1 vs. dc1	72.000	−1.329	0.195	27.000	0.542	0.633
di2 vs. dc1	33.000	−1.683	0.094	17.000	−0.963	0.336
	Cuspal outer region			Lateral outer region		
di1 vs. di2	11.000	−0.570	0.648	2.000	−1.414	0.229
di1 vs. dc1	23.000	−0.579	0.613	6.000	−1.710	0.109
di2 vs. dc1	10.500	−0.936	0.368	12.000	0.000	1.000

TABLE A2. Comparing maxillary anterior tooth enamel DSRs between tooth types

	U	*Z*	*P*	*U*	*Z*	*P*
	Cuspal inner region			Lateral inner region		
di1 vs. di2	20.500	−1.418	0.161	14.000	−0.341	0.808
di1 vs. dc1	82.000	−0.151	0.902	4.000	−1.482	0.194
di2 vs. dc1	110.500	0.000	1.000	8.500	−1.276	0.214
	Cuspal mid region			Lateral mid region		
di1 vs. di2	9.000	−1.610	0.103	11.000	−0.314	0.841
di1 vs. dc1	5.000	−1.881	0.073	21.500	−1.251	0.219
di2 vs. dc1	63.000	−0.500	0.644	15.500	−1.677	0.095
	Cuspal outer region			Lateral outer region		
di1 vs. di2	15.000	−1.000	1.000	–	–	–
di1 vs. dc1	35.500	−1.234	0.226	–	–	–
di2 vs. dc1	40.000	−0.934	0.378	10.000	−1.681	0.073

TABLE A3. Comparing anterior tooth enamel DSRs within tooth types

	di1		di2		dc1	
Cusp vs. lateral	*Z*	*P*	*Z*	*P*	*Z*	*P*
Mandibular						
Inner vs. inner	0.000	1.000	−0.105	0.917	−1.095	0.273
Mid vs. mid	−1.753	0.800	−0.338	0.735	−1.490	0.136
Outer vs. outer	−1.000	0.317	−0.535	0.593	−0.365	0.715
Maxillary						
Inner vs. inner	−1.461	0.144	−0.700	1.753	−0.271	0.786
Mid vs. mid	−2.032	0.046*	−0.484	0.080	−0.405	0.686
Outer vs. outer	–	–	−0.552	0.581	−1.095	0.273

TABLE A4. Comparing anterior mandibular vs. maxillary DSRs

	Cuspal			Lateral		
	U	*Z*	*P*	*U*	*Z*	*P*
		di1			di1	
Inner	35.000	0.000	1.000	4.000	−0.720	0.629
Mid	24.500	−0.580	0.574	12.500	0.000	1.000
Outer	2.000	−2.132	0.058	–	–	–
		di2			di2	
Inner	52.500	−1.387	0.168	19.000	−0.646	0.573
Mid	17.000	−2.044	0.053	11.000	−1.123	0.310
Outer	6.000	−1.868	0.073	50.000	−1.347	0.188
		dc1			dc1	
Inner	63.000	−2.437	0.014*	4.000	−1.480	0.190
Mid	109.000	−0.203	0.857	73.000	−0.874	0.402
Outer	61.000	−0.611	0.541	4.000	−1.162	0.343

TABLE A5. Comparing mandibular and maxillary CFTs

	U	*Z*	*P*
di_2 vs. di^2	31.500	−1.399	0.162
dc_1 vs. dc^1	88.500	−1.489	0.136

LITERATURE CITED

Antoine D, Hillson S, Dean MC. 2009. The developmental clock of dental enamel: a test for the periodicity of prism cross-striations and an evaluation of the likely sources of error in histological studies of this kind. J Anat 214:45–55.

von Asper H. 1916. Über die Braune Retzius'sche Parallelstreifung im Schmelz der menschlichen Zähne. Thesis (doctoral), Universität Zürich.

Beynon AD. 1992. Circaseptan rhythms in enamel development in modern humans and Plio-Pleistocene hominids. In: Smith P and Tchernov E, editors. Structure, function and evolution of teeth. London: Freund Publishing House. p 295–309.

Beynon AD, Reid DJ. 1987. Relations between perikymata counts and crown formation times in the human permanent dentition. J Dent Res 66:889–890.

Beynon AD, Clayton CB, Ramirez Rozzi FV, Reid D. 1998a. Radiographic and histological methodologies in estimating the chronology of crown development in modern humans and great apes: a review, with some applications for studies on juvenile hominids. J Hum Evol 35:351–370.

Beynon AD, Dean MC, Leakey MG, Reid DJ, Walker A. 1998b. Comparative dental development and microstructure of Proconsul teeth from Rusinga Island, Kenya. J Hum Evol 35:163–209.

Beynon AD, Dean MC, Reid DJ. 1991a. Histological study on the chronology of the developing dentition in gorilla and orangutan. Am J Phys Anthropol 86:189–203.

Beynon AD, Dean MC, Reid DJ. 1991b. On thick and thin enamel in hominoids. Am J Phys Anthropol 86:295–309.

Birch W, Dean MC. 2009. Rates of enamel formation in human deciduous teeth. In: Koppe T, Meyer G, Alt K, editors. Comparative dental morphology. Front Oral Biol. Basel: Karger. p 116–120.

Boyde A. 1964a. The structure and development of mammalian enamel. PhD thesis. University of London. London, UK.

Boyde A. 1964b. Estimation of age at death of young human skeletal remains from incremental lines in dental enamel. Third International Meeting in Forensic Immunology, Medicine, Pathology and Toxicology, Plenary Session 11A. London, April 16–24, 1963. Excerpta Med Int Congr Ser , Vol.80.

Boyde A. 1979. Carbonate concentration, crystal centres, core dissolution, caries, cross striation, circadian rhythms and compositional contrast in the SEM. J Dent Res 58:981–983.

Boyde A. 1989. Enamel. In: Berkovitz BKB, Boyde A, Frank RM, Hohling HJ, Moxham BJ, Nalbandian J, Tonge CH, editors. Teeth. Handbook of microscopic anatomy. Berlin: Springer-Verlag. p 309–473.

Bromage TG. 1991. Enamel incremental periodicity in the pigtailed macaque: a polychrome fluorescent labelling study of dental hard tissues. Am J Phys Anthropol 86:205–214.

Bromage TG, Dean MC. 1985. Re-evaluation of the age at death of immature fossil hominids. Nature 317:525–527.

Bromage TG, Lacruz RS, Hogg R, Goldman HM, McFarlin SC, Warshaw J, Dirks W, Perez Ochoa A, Smolyar I, Enlow DH, Boyde A. 2009. Lamellar bone is an incremental tissue reconciling enamel rhythms, body size, and organismal life history. Calcif Tiss Int 84:388–404.

Butler PM. 1992. Correlative growth on upper and lower tooth germs in human foetus. Ann Zool Fennici 28:261–271.

Dean, MC. 1987a. The dental developmental status of six East African juvenile fossil hominids. J Hum Evol 16:197–213.

Dean MC. 1987b. Growth layers and incremental markings in hard tissues; a review of the literature and some preliminary observations about enamel structure in *Paranthropusboisei*. J Hum Evol 16:157–172.

Dean MC. 1998. A comparative study of cross striation spacings in cuspal enamel and of four methods of estimating the time taken to grow molar cuspal enamel in *Pan, Pongo*, and *Homo*. J Hum Evol 35:449–462.

Dean MC, Beynon AD. 1991. Histological reconstruction of crown formation times and initial root formation times in a modern human child. Am J Phys Anthropol 86:215–228.

Dean MC, Scandrett AE. 1996. The relationship between long-period incremental markings in dentine and daily cross striations in enamel in human teeth. Arch Oral Biol 41:233–241.

Dean MC, Beynon AD, Thackeray JF, Macho GA. 1993. Histological reconstruction of dental development and age at death of a juvenile *Paranthropus robustus* specimen, SK 63, from Swartkrans, South Africa. Am J Phys Anthropol 91:401–419.

Dean MC, Leakey MG, Reid DJ, Schrenk F, Schwartz GT, Stringer C, Walker AC. 2001. Growth processes in teeth distinguish modern humans from *Homo erectus* and earlier hominins. Nature 414:628–631.

Dean MC, Stringer CB, Bromage TG. 1986. Age at death of the Neanderthal child from Devils Tower, Gibraltar and the implications for studies of general growth and development in Neanderthals. Am J Phys Anthropol 70:301–309.

Dirks W. 1998. Histological reconstruction of dental development and age at death in a juvenile gibbon (*Hylobateslar)*. J Hum Evol 35:411–425.

Dirks W. 2003. Effect of diet on dental development in four species of catarrhine primates. Am J Primatol 61:29–40.

Dirks W, Bowman JE. 2007. Life history theory and dental development in four species of catarrhine primates. J Hum Evol 53:309–320.

Fanning EA. 1961. A longitudinal study of tooth formation and root resorption. N Z Dent J 57:202–217.

Fanning EA, Brown T. 1971. Primary and permanent tooth development. Austral Dent J 16:41–43.

FitzGerald CM. 1996. Tooth crown formation and the variation of enamel microstructural growth markers in modern humans. PhD thesis. University of Cambridge. Cambridge, UK.

FitzGerald CM. 1998. Do enamel microstructures have regular time dependency? Conclusions from the literature and a large-scale study. J Hum Evol 35:371–386.

FitzGerald CM, Hillson S. 2009. Deciduous tooth growth in an ancient Greek infant cemetery. In: Koppe T, Meyer G, Alt K, editors. Comparative dental morphology. Front Oral Biol. Basel: Karger. p 178–183.

FitzGerald CM, Saunders SR. 2005. Test of histological methods of determining chronology of accentuated striae in deciduous teeth. Am J Phys Anthropol 127:277–290.

FitzGerald C, Saunders S, Bondioli L, Macchiarelli R. 2006. Health of infants in an Imperial Roman skeletal sample: perspective from dental microstructure. Am J Phys Anthropol 130:179–189.

FitzGerald CM, Saunders SR, Macchiarelli R, Bondioli L. 1999. Large scale histological assessment of deciduous crown formation. In: Mayhall JT, editor. Dental morphology 98. Oulu, Finland: University of Oulu Proceedings of the 11th International Symposium on Dental Morphology. p 92–101.

Folayan M, Owotade F, Adejuyigbe E, Sen S, Lawal B, Ndukwe K. 2007. The timing of eruption of the primary dentition in Nigerian children. Am J Phys Anthropol 134:443–448.

Fukuhara T. 1959. Comparative anatomical studies of the growth lines in the enamel of mammalian teeth. Acta Anat Nipp 34:322–332.

Garn SM, Burdi AR. 1971. Prenatal ordering and postnatal sequence in dental development. J Dent Res 50:1407–1414.

Godfrey LR, Samonds KE, Jungers WL, Sutherland MR. 2001. Teeth, brains, and primate life histories. Am J Phys Anthropol 114:192–214.

Gustafson AG. 1959. A morphologic investigation of certain variations in the structure and mineralization of human dental enamel. Odontolog Tidsk 67:366–472.

Gwinnett AJ. 1966. The ultrastructure of the prismless enamel of deciduous teeth. Arch Oral Biol 12:381–387.

Hicks J, Hicks J. 2000. St Gregory's Priory, Northgate: excavations 1989–1991. Canterbury: Canterbury Archaeological Trust.

Hitchcock NE, Gilmour AI, Gracey M, Kailis DG. 1984. Australian longitudinal study of time and order of eruption of primary teeth. Comm Dent Oral Epidemiol 12:260–263.
Holman DJ, Yamaguchi K. 2005. Longitudinal analysis of deciduous tooth emergence: IV. Covariate effects in Japanese children. Am J Phys Anthropol 126:352–358.
Huda T, Bowman JE. 1994. Variation in cross-striation number between striae in an archaeological population. Int J Osteoarchaeol 4:49–52.
Huda T, Bowman JE. 1995. Age determination from dental microstructure in juveniles. Am J Phys Anthropol 97: 135–150.
Katzenberg MA, Oetelaar G, Oetelaar J, FitzGerald CM, Yang D, Saunders SR. 2005. Identification of historical human skeletal remains: a case study using skeletal and dental age, history and DNA. Int J Osteoarchaeol 15:61–72.
Kawasaki K, Tanaka S, Ishikawa T. 1979. On the daily incremental lines in human dentine. Arch Oral Biol 24:939–943.
Kraus BS. 1959a. Differential calcification rates in the human primary dentition. Arch Oral Biol 1:133–144.
Kraus BS. 1959b. Calcification of the human deciduous teeth. J Am Dent Assoc 59:1128–1136.
Kraus BS, Jordan R. 1965. The human dentition before birth. Philadelphia: Lea and Febiger.
Lacruz RS, Bromage TG. 2006. Appositional enamel growth in molars of South African fossil hominoids. J Anat 209:13–20.
Lacruz, RS, Dean, MC, Ramirez-Rozzi F, Bromage TG. 2008. Megadontia, striae periodicity and patterns of enamel secretion in Plio-Pleistocene fossil hominins. J Anat 213:148–158.
Lacruz RS, Ramirez Rozzi F, Bromage TG. 2006. Variation in enamel development of South African fossil hominids. J Hum Evol 51:580–590.
Liversidge HM, Molleson TI. 2004. Variation in crown and root formation and eruption of human deciduous teeth. Am J Phys Anthropol 123:172–180.
Logan WHG, Kronfeld R. 1933. Development of the human jaws and surrounding structures from birth to age fifteen. J Am Dent Assoc 20:379–427.
Lysell L, Magnusson B, Thilander B. 1962. Time and order of eruption of the primary teeth. A longitudinal study. Odontol Rev 13:217–234.
Macchiarelli R, Bondioli L, Debenath A, Mazurier A, Tournepiche JF, Birch W, Dean C. 2006. How Neanderthal molar teeth grew. Nature 444:748–751.
Macho GA, Reid DJ, Leakey MG, Jablonski N, Beynon AD. 1996. Climatic effects on dental development of *Theropithecus oswaldi* from KoobiFora and Olorgesailie. J Hum Evol 30:57–70.
Mahoney P. 2008. Intraspecific variation in M_1 enamel development in modern humans: implications for human evolution. J Hum Evol 55:130–146.
Mahoney P. 2010. Two dimensional patterns of human enamel thickness on deciduous (dm1, dm2) and permanent first (M1) mandibular molars. Arch Oral Biol 55:115–126.
Mahoney P. 2011. Human deciduous mandibular molar incremental enamel development. Am J Phys Anthropol 144:204–214.
Mahoney P, Smith T, Schwartz G, Dean C, Kelley J. 2007. Molar crown formation in the late Miocene Asian hominoids, *Sivapithecus parvada, Sivapithecus sivalensis*. J Hum Evol 53:61–68.
Martin LB. 1983. The relationships of the later Miocene Hominoidea. Ph.D. thesis. University College London. London, UK.
Mimura T. 1939. Horoshitsu ni mirareru Seicho-sen no shuki. "The periodicity of growth lines seen in enamel." Kobyo-shi 13:454–455.
Moorrees CFA, Fanning EA, Hunt EE. 1963. Formation and resorption of three deciduous teeth in children. Am J Phys Anthropol 19:99–108.
Nomata N. 1964. A chronological study on the crown formation of the human deciduous dentition. Bull Tokyo Med Dent Univ 11:55–76.
Ohtsuka M, Shinoda H. 1995. Ontogeny of circadian dentinogenesis in the rat incisor. Arch Oral Biol 40:481–485.
Osborn JW. 1973. Variations in structure and development of enamel. Oral Sci Rev 3:3–83.
Reid DJ, Dean MC. 2000. Brief communication: the timing of linear hypoplasias on human anterior teeth. Am J Phys Anthropol 113:135–139.
Reid DJ, Dean MC. 2006. Variation in modern human enamel formation times. J Hum Evol 50:329–346.
Reid DJ, Ferrell R. 2006. The relationship between number of striae of Retzius and their periodicity in imbricational enamel formation. J Hum Evol 50:195–202.
Reid DJ, Beynon AD, Ramirez Rozzi FV. 1998a. Histological reconstruction of dental development in four individuals from a medieval site in Picardie, France. J Hum Evol 35:463–477.
Reid DJ, Schwartz GT, Dean MC, Chandrasekera MS. 1998b. A histological reconstruction of dental development in the common chimpanzee, *Pan troglodytes*. J Hum Evol 35:427–448.
Retzius A. 1837. Bemerkungenq ber den inneren Bau der Zähne, mit besonderer Rücksicht auf dem in Zahnknochen Vorkommenden Röhrenbau. Arch Anat Physiol 486–566.
Ripa LW. 1966. The histology of the early carious lesion in primary teeth with special reference to a prismless outer layer of primary enamel. J Dent Res 45:5–11.
Risnes S. 1986. Enamel apposition rate and the prism periodicity in human teeth. Scand J Dent Res 94:394–404.
Risnes S. 1990. Structural characteristics of staircase-type Retzius lines in human dental enamel analyzed by scanning electron microscopy. Anat Rec 226:135–146.
Roche AF, Barkla DH, Maritz JD. 1964. Deciduous eruption in Melbourne children. Austral Dent J 2:106–108.
Rosenberg GD, Simmons DJ. 1980. Rhythmic dentinogenesis in the rabbit incisor: circadian, ultradian, and infradian periods. Cal Tiss Int 32:29–44.
Rushton MA. 1933. Fine contour lines of enamel milk teeth. Dent Res 53:170–171.
Sabel N, Johansson C, Kuhnisch J, Robertson A, Steiniger F, Norén JG, Klingberg G, Nietzsche S. 2008. Neonatal lines in the enamel of primary teeth—a morphological and scanning electron microscopic investigation. Arch Oral Biol 53:954–963.
Schour I. 1936. Neonatal line in enamel and dentin of human deciduous teeth and first permanent molar. J Dent Res 18:91–102.
Schour I, Poncher HG. 1937. Rate of apposition of enamel and dentin, measured by the effect of acute fluorosis. Am J Dis Child 54:757–776.
Schwartz GT, Godfrey LR, Mahoney P. 2007. Inferring primate growth, development, and life history from dental microstructure: the case of the extinct giant Malagasy lemur. In: Bailey S, Hublin J-J, editors. Dental perspectives on human evolution. Dordrecht: Kluwer Academic Publishers. p 69–81.
Schwartz GT, Liu W, Zheng L. 2003. Preliminary investigation of dental microstructure in the Yuanmou hominoid (*Lufengpithecus hudienensis*). Yunnan Province, China. J Hum Evol 44:189–202.
Schwartz GT, Mahoney P, Godfrey LR, Cuozzo FP, Jungers WL, Randria GFN. 2005. Dental development in *Megaladapis edwardsi* (Primates, Lemuriformes): implications for understanding life history variation in sub-fossil lemurs. J Hum Evol 49:702–721.
Schwartz GT, Reid DJ, Dean MC. 2001. Developmental aspects of sexual dimorphism in hominoid canines. Int J Primatol 22:837–860.
Schwartz GT, Reid DJ, Dean MC, Zihlman AL. 2006. A faithful record of stressful life events preserved in the dental developmental record of a juvenile gorilla. Int J Primatol 27: 1201–1222.
Schwartz GT, Samonds K, Godfrey LR, Jungers W, Simons E. 2002. Dental microstructure and life history in subfossil Malagasy lemurs. Proc Natl Acad Sci USA 99:6124–6129.
Shellis RP. 1984. Variations in growth of the enamel crown in human teeth and a possible relationship between growth and enamel structure. Arch Oral Biol 29:697–705.
Shellis RP, Poole DFG. 1977. The calcified dental tissues of primates. In: Lavelle CLB, Shellis RP, Poole DFG, editors. Evolutionary changes to the primate skull and dentition. Springfield, IL: Charles C. Thomas. p 197–279.

Smith BH, Crummett L, Brandt KL. 1994. Ages of eruption of primate teeth: a compendium for aging individuals and comparing life histories. Yearb Phys Anthropol 37:177–231.
Smith TM. 2004. Incremental development of primate dental enamel. Ph.D. thesis. Stony Brook University, New York, USA.
Smith TM. 2006. Experimental determination of the periodicity of incremental features in enamel. J Anat 208:99–114.
Smith TM. 2008. Incremental dental development: methods and applications in hominoid evolutionary studies. J Hum Evol 54:205–224.
Smith TM, Martin LB, Sirianni JE. 2002. Incremental features of pre- and postnatal enamel microstructure in pigtailed macaques (*Macaca nemestrina*). Am J Phys Anthropol Suppl 34:144.
Smith TM, Reid DJ, Dean MC, Olejniczak AJ, Martin LB, 2007a. Molar development in common chimpanzees (*Pan troglodytes*). J Hum Evol 52:201–216.
Smith TM, Reid DJ, Sirianni JE. 2006. The accuracy of histological assessments of dental development and age at death. J Anat 208:125–138.
Smith TM, Tafforeau PT, Reid DJ, Grün R, Eggins S, Boutakiout M, Hublin JJ. 2007b. Earliest evidence of modern human life history in North African early *Homo sapiens*. Proc Natl Acad Sci USA 104:6128–6133.
Sunderland EP, Smith CJ, Sunderland R. 1987. A histological study of the chronology of initial mineralization in the human deciduous dentition. Arch Oral Biol 32:167–174.
Weber DF, Eisenmann DR. 1971. Microscopy of the neonatal line in developing human enamel. Am J Anat 132:375–391.
Woodroffe S, Mihailidis S, Hughes T, Bockmann M, Seow WK, Gotjamanos T, Townsend G. 2010. Primary tooth emergence in Australian children: timing, sequence and patterns of asymmetry. Austral Dent J 55:245–251.